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CONSUMPTION OF DIFFUSE KNAPWEED BY TWO SPECIES OF POLYPHAGOUS GRASSHOPPERS (ORTHOPTERA: ACRIDIDAE) IN SOUTHERN IDAHO

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ABSTRACT.—Consumption of diffuse knapweed (*Centaurea diffusa* Lam.) by 2 polyphagous grasshopper species, *Melanoplus sanguinipes* (F.) and *Oedaleonotus enigma* (Scudder), was studied using microhistological analysis of grasshopper crop contents. Grasshoppers were confined to cages containing *C. diffusa* and *Sisymbrium altissimum* L., a member of the mustard family known to be readily eaten by these 2 grasshopper species. Preference indices for knapweed were lower than for *S. altissimum* in 4 of 5 trials. An uncaged population of *M. sanguinipes* on a knapweed-infested site consumed only small amounts of knapweed until late summer when most other plants were senescent. Results suggest that diffuse knapweed's low palatability to generalist herbivores may confer to it a competitive advantage over other rangeland plants.

Key words: Centaurea diffusa *Lam., diffuse knapweed, herbivory, insects, competition.*

Diffuse and spotted knapweed, *Centaurea diffusa* Lam. and *C. maculosa* Lam., respectively, were introduced to the Pacific Northwest around 1900 (Watson and Renney 1974). Since then they have rapidly spread throughout the area (Fig. 1; Forcella and Harvey 1981). Heavy infestations of knapweed reduce production of more desirable species of forage plants, thus reducing the value of rangeland for grazing and wildlife habitat. Several specialist insect herbivores have been introduced in attempts to control knapweed (Story and Anderson 1978, Maddox 1979). To date, no studies have reported on the consumption of knapweed by polyphagous insect herbivores.

Cnicin, a sesquiterpene lactone, is produced by spotted and diffuse knapweed (Drodz 1966, Locken and Kelsey 1987). Picman (1986) suggested that sesquiterpene lactones have toxic effects on many herbivores and may function as deterrents to herbivory. Locken and Kelsey (1987) suggested that nonpalatability of knapweeds may afford them a competitive advantage over many other plant species by protecting them from herbivory. Grasshoppers (Orthoptera: Acrididae) are a conspicuous and important class of herbivores on rangeland in the western U.S.

Rangeland grasshopper populations in southern Idaho occasionally reach outbreak proportions. Two species in particular, *Melanoplus sanguinipes* (F). and *Oedaleonotus enigma* (Scudder), are capable of attaining very high densities (>30/m²). Both species feed upon a broad range of forbs (Brusven and Lamley 1971, Banfill and Brusven 1973, Sheldon and Rogers 1978). Pfadt (1992) suggested that an increase in introduced weeds is a factor leading to outbreaks of *O. enigma.* Fielding and Brusven (1993) found that both species prefer disturbed rangeland habitats dominated by exotic annual plants. This study assessed the utilization of diffuse knapweed as food by these 2 grasshopper species to determine if knapweed represents a significant and expanding resource for grasshoppers and if grasshopper herbivory may be a constraint to knapweed populations.

Previous studies (Brusven and Lamley 1971) have shown *Sisymbrium altissimum* L., an introduced annual forb, to be preferred by many forb-feeding grasshoppers. Both species of weeds initiate growth as a basal rosette of leaves and later develop erect, sparsely leaved stems that bear flowers. Because *C. diffusa* is usually a biennial, it does not develop beyond the basal rosette until the 2nd year. *Sisymbrium altissimum* constituted a large proportion of the forbs present in this study; therefore utilization of *C. diffusa* and *S. altissimum* was compared.

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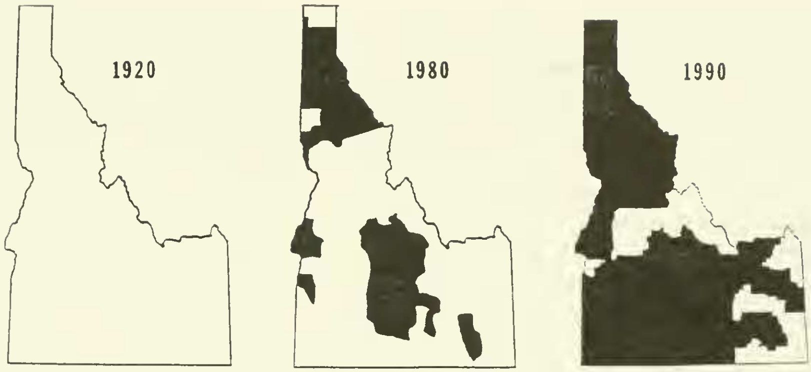

Fig. 1. Idaho counties reporting infestations of diffuse knapweed, *Centaurea diffusa*.

Materials and Methods

The study site is about 3 km south of Shoshone, Idaho (Lincoln County), in a knapweed-infested area that had been seeded with crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) in 1975. Grasshopper food preferences were identified by microhistological analysis of grasshopper crop contents (Brusven and Mulkern 1960, Sparks and Malechek 1968, Fielding and Brusven 1992). Grasshoppers were confined to cages so that relative amounts of different plant species could be precisely determined. Five trials were conducted during the summer of 1989: *O. enigma* 4th- and 5th-instar nymphs in early June; *O. enigma* adults and *M. sanguinipes* 4th and 5th instars in late June; *M. sanguinipes* adults in July and again in August. For each trial, 4 wire-mesh (5-mm pore size), conical cages covering 0.5 m^2 each were placed in the field such that at least 1 plant each of *C. diffusa* and *Sisymbrium altissimum* L., along with assorted common grasses, occurred within each cage. Twelve to 15 grasshoppers of a single species were placed in each cage. Grasshoppers used in the tests were collected from rangeland and placed in the cages within 20 h of collection. A 4-d interval was estimated to be sufficient to completely void previous meals and to accurately assess preferences in choice tests. After 4 d, 10 grasshoppers were removed from each cage and immediately preserved in 95% ethanol for crop analysis.

Species composition of plants in each cage was determined on an air-dry basis by clipping and sorting by species aboveground portions of plants in each cage after each trial. Clipped plants were stored in air-tight plastic bags, and fresh weight was obtained within 4 h of clipping. Clipped plants were then allowed to air-dry until they quit losing weight (10–15 d), after which dry weights were obtained (to the nearest 0.1 g). Percent moisture of aboveground portions of each plant species was then determined.

Plants were rated after each trial according to phenology as follows: 1, vegetative growth only; 2, flowering; 3, seed set; 4, seed maturity; 5, senescent or dormant (USDA–Soil Conservation Service 1976). Grass species present included *Poa sandbergii* Vasey, *Bromus tectorum* L., and *Agropyron cristatum*. *Centaurea diffusa* and *S. altissimum* composed about 97% of aboveground biomass of forbs. Both 1st- and 2nd-year *C. diffusa* were present in each of the cages. Other forbs present were *Helianthus annuus* L., *Lactuca serriola* L., and *Epilobium* L. sp.

Grasshopper crops were removed and the contents mounted on glass slides in glycerin and safranin stain. Plant fragments in the crops were identified by comparing them with reference slides made from fragments of known plants collected at the study site, similar to the methods described by Fielding and Brusven (1992). Frequency counts were made for each plant species by determining their presence or absence in 20 microscope viewing fields per grasshopper crop. Trichomes, hairs, and pollen were not counted. Frequencies from the 10 grasshoppers per cage were summed. Relative frequency was calculated by dividing the frequency of a plant species by the total frequency of all plant species (Sparks and Malechek 1968, Pfadt and Lavigne 1982). Holecheck and Gross (1982) demonstrated the near equivalence of relative frequency to actual dry weight percentage of plants consumed.

Relative availability of different plant species within an area has been shown to influence diet composition in many grasshopper species (Ueckert et al. 1972, Mitchell 1975). To account for the effect of availability on consumption, preference values for plant species constituting more than 10% of either cage or crop contents were calculated by dividing relative frequency of a plant species in the crops by that species' percentage of the dry-weight of all plants within the cages (Ueckert and Hansen 1971). A preference value >1 indicates feeding in greater proportion to the plant's availability, whereas a preference value <1 indicates low preference in relation to a plant's availability.

Possibly, total dry weight of a plant may not accurately portray the amount of plant material available to grasshoppers, thus introducing bias into the preference values. In this study our observations indicated that both species of weeds had similar ratios of leaves to stems. Also, we have observed grasshoppers feeding on stems of both weed species. Because we had no way to determine more precisely exactly what proportion of the plant was available as food to the grasshoppers, we used total aboveground biomass as a reasonably objective measure of availability. The presence of 1st-year rosettes of *C. diffusa* in the cages ensured that each replication included a representative choice of plant material.

Differences between plant species in relative frequency and preference values were tested using the Wilcoxon 2-sample test (PROC NPAR1WAY, SAS 1985), with each cage representing 1 replication. Comparisons between plant species were made for each trial of a single grasshopper species and with data from different trials pooled by grasshopper species. The same statistical methods were also used to test for differences in relative frequency and preference values between grasshopper species for *C. diffusa* and *S. altissimum*.

Food selection was monitored in an uncaged population of *M. sanguinipes* near the cage study. Thirty to 50 individuals were collected on each of 5 dates from June through October from an area of ca 1 ha infested with knapweed. Food preference in this population was determined by microhistological methods described above.

Plant species composition at the site was determined by visual estimates, in 5% increments, of the ground cover of each plant species in forty 0.1-m^2 quadrats, arranged in 4 transects of 10 quadrats each. Ground cover estimates were made in July and again in October after precipitation caused abundant germination of cheatgrass. Because accurate estimates of food availability (biomass) in the field were not available, preference values were not calculated and the results are presented for comparative purposes only.

RESULTS

Cages were placed such that *C. diffusa* was equally as abundant as or more abundant than *S. altissimum* in each trial (Table 1). Percentage moisture of both species of weeds declined throughout the season (Table 1). *Sisymbrium altissimum* tended to be slightly more advanced phenologically than *C. diffusa* throughout the season, partly due to the presence of 1st-year rosettes of *C. diffusa* in the cages, but also because of earlier flowering by *S. altissimum* (Table 1).

Although *C. diffusa* constituted a substantial percentage (10–46%) of the caged grasshoppers' diet, preference values for *C. diffusa* were <1 in every trial, indicating that it was not consumed in proportion to its dry weight composition within the cages (Table 1). Preferences values for *S. altissimum* were >1 in each trial, indicating that it was consumed in proportions greater than its relative availability.

After flowering in July, a large portion of the *C. diffusa* plant material in the crops of *M. sanguinipes* consisted of floral parts (44% and 30% of the *C. diffusa* material consumed, in the July and August trials, respectively). Other forbs represented in in situ caged trials were not present in sufficient quantity to adequately assess their preference values.

More *S. altissimum* than *C. diffusa* was consumed by grasshoppers in 3 of the 5 trials (Table 1). Preference values for *S. altissimum* were greater than those for *C. diffusa* in 4 of the trials (Table 1). Combining data from the 3 trials with *M. sanguinipes*, crop contents and preference values for *S. altissimum*, 42% and 2.0, respectively, were greater than for *C. diffusa*, 16% and 0.5, respectively (Wilcoxon test, $P < 0.01$ for both tests). For *O. enigma*, the overall preference value for *S. altissimum*, 3.5,

TABLE 1. Relative availability and consumption by grasshoppers of plant species.

Plant species	Plant phenological stage[1]	Percent moisture of plants	Mean dry weight in cages	Relative availability in cages[2]	Relative frequency in crops	Mean preference index
4th- and 5th-instar *Oedaleonotus enigma* nymphs on 6 June 1989						
Centaurea diffusa	1	77	13.4	23	10a[3]	0.38a
Sisymbrium altissimum	1	81	8.8	15	48b	5.06b
Other forbs	1	85	0.6	1	<1	—
Agropyron cristatum	1–2	57	18.1	31	<1	<0.05
Poa sandbergii	4	24	4.7	8	2	—
Bromus tectorum	4	21	12.8	22	32	1.42
Detritus					6	
adult *Oedaleonotus enigma* on 26 June 1989						
Centaurea diffusa	1	64	59.0	61	46a	0.76a
Sisymbrium altissimum	1–2	67	27.1	28	48a	1.93a
Other forbs	1–2	79	1.0	1	1	—
Agropyron cristatum	3–4	45	6.8	7	0	—
Poa sandbergii	5	15	0	0	0	—
Bromus tectorum	5	12	3.6	3	1	—
Detritus					4	—
4th- and 5th-instar *Melanoplus sanguinipes* nymphs on 26 June 1989						
Centaurea diffusa	1	64	60.8	59	16a	0.25a
Sisymbrium altissimum	1–2	67	25.8	25	74b	3.00b
Other forbs	1–2	79	2.1	2	0	—
Agropyron cristatum	3–4	45	6.2	6	0	—
Poa sandbergii	5	15	4.1	4	5	—
Bromus tectorum	5	12	3.1	3	4	—
Detritus					2	—
adult *Melanoplus sanguinipes* on 21 July 1989						
Centaurea diffusa	1–2	63	25.4	29	16a	0.56a
Sisymbrium altissimum	2–3	55	24.5	28	44b	1.55b
Other forbs	1–2	75	8.8	1	3	—
Agropyron cristatum	4	45	7.0	8	4	—
Poa sandbergii	5	9	17.5	20	3	0.17
Bromus tectorum	5	14	11.4	13	27	2.52
Detritus					3	—
adult *Melanoplus sanguinipes* on 25 August 1989						
Centaurea diffusa	1, 3–4	22	38.8	38	23a	0.70a
Sisymbrium altissimum	4–5	11	18.4	18	24a	1.48b
Other forbs	2–3	65	8.2	8	5	—
Agropyron cristatum	4	18	15.3	15	3	0.37
Poa sandbergii	5	8	4.1	4	5	—
Bromus tectorum	5	7	13.3	13	25	2.83
Detritus					16	—

[1]1, vegetative growth only; 2, flowering; 3, seed set; 4, seed maturity; 5, senescent or dormant
[2]Mean ($N = 4$) percentage of aboveground plant biomass (air-dry basis) within cages
[3]Means for *C. diffusa* and *S. altissimum* within columns of each trial followed by different letters are significantly different, $P < 0.05$, Wilcoxon 2-sample test.

was greater than for *C. diffusa*, 0.6 (Wilcoxon test, $P < 0.05$). There was no difference in consumption by *O. enigma* between *S. altissimum* and *C. diffusa*, 48% and 27%, respectively (Wilcoxon test, $P > 0.05$). There were no differences between the 2 species of grasshoppers in relative frequency or preference values for either *S. altissimum* or *C. diffusa* (Wilcoxon test, $P > 0.10$ for both comparisons).

Of the grass species, only *Bromus tectorum* was eaten in greater proportion than its percentage of air-dry biomass. Even though *O. enigma* is generally considered to be a forb-feeder (Sheldon and Rogers 1978, Pfadt 1992), *B. tectorum* constituted 32% of the diet of *O. enigma* in early June (Table 1). Adult *O. enigma* in late June ate very little *B. tectorum*. *Melanoplus sanguinipes* consumed *B. tectorum* throughout the summer, with 4–27% of its diet composed of *B. tectorum*, even though the grass was completely senescent by 26 June (Table 1).

TABLE 2. Relative frequency of food items in crops of *M. sanguinipes* on 5 dates and percentage ground cover in July and October 1989.

	Relative frequency of crop components					Percentage ground cover	
	30 June	20 July	14 Aug	6 Sep	13 Oct	July	October
Sisymbrium altissimum	46	23	22	7	6	2	1
Centaurea diffusa	18	30	32	55	1	6	4
Other forbs[a]	19	25	7	24	6	<1	<1
Bromus tectorum	7	9	12	6	76	5	16
Other grasses	1	4	15	1	10	5	6
Litter, detritus	9	9	13	7	1		

[a]Includes rabbitbrush (*Chrysothamnus nauseosus* [Pall.] Britt.), lupine (*Lupinus* L. sp.), and sunflower (*Helianthus annuus* L.)

Knapweed was the most common forb growing on the site where the uncaged population of *M. sanguinipes* was studied (Table 2). In June, *S. altissimum* was the largest single food item, but consumption declined as the season progressed. Knapweed was a substantial food item, especially in August and September when it remained succulent after other forbs had dried. After rainfall stimulated germination of *B. tectorum* in late September and October (Table 2), it became the primary food item for *M. sanguinipes*, and forbs constituted only a minor portion of the diet.

DISCUSSION

The evolutionary history of an herbivorous species, by shaping its food habits and other life history traits, determines its present relationships with exotic plant species. The 2 grasshopper species in this study consume a wide variety of plants, especially forbs (Banfill and Brusven 1973, Sheldon and Rogers 1978, Pfadt 1992), and will readily accept exotic plant species. *Melanoplus sanguinipes* is a very opportunistic feeder. Egg hatch in this species is often spread out over a long period, resulting in a large proportion of a population maturing during the dry periods typical of late summer in the intermountain region. At such times many late-maturing plants that still retain some succulence, such as rabbitbrush, sagebrush, and some lupine species, are primary food items for *M. sanguinipes*. The results of this study indicate that this was the case with *C. diffusa*; even though it was not highly preferred by *M. sanguinipes*, it was a major food item in late summer when most other plants were dry. *Sisymbrium altissimum* tended to become senescent earlier than *C. diffusa*, which would reduce the quality of *S. altissimum* relative to *C. diffusa*, especially when 1st-year rosettes, consisting mostly of leaves, are considered.

Locken and Kelsey (1987) reported that cnicin concentrations in *C. maculosa* vary considerably within and among individual knapweed plants. Cnicin is stored within glandular trichomes on the surface of knapweed tissues. Highest concentrations of cnicin were found in leaves surrounding the inflorescence. Only trace quantities were found by Locken and Kelsey (1987) in the stem epidermis and flowers. Leaf concentrations were lowest in spring and increased with flowering. We assume that cnicin concentrations in *C. diffusa* follow much the same pattern. Variability in cnicin concentration may result in selective consumption by grasshoppers of knapweed tissues with low cnicin concentrations. Our results suggest that this is the case: In late-summer trials much of the knapweed tissue consumed by grasshoppers consisted of flowers. This implies that during years of high grasshopper densities, feeding by grasshoppers, especially on the flowers, could result in a modest reduction in seed production in this plant.

Results of this study provide support for the hypothesis that knapweed is protected from herbivory by its chemical constituents (Picman 1986, Locken and Kelsey 1987). When compared to *S. altissimum*, diffuse knapweed was a 2nd-choice food item for these generalist grasshopper species. Its low palatability may confer a competitive advantage to knapweed when herbivory is a strong selection factor. Although it is conceivable that at high densities grasshoppers may consume significant amounts of knapweed and reduce seed production, many other plants would be affected to a greater degree, thus reducing competition to knapweed.

Grasshopper species used in this trial are the dominant species contributing to outbreaks in southern Idaho. It appears that increasing knapweed infestations do not represent a significant increase in food resources for these grasshoppers. However, because knapweed stays green longer during the summer than many other rangeland plants, it may provide sustenance for polyphagous grasshoppers during late-summer droughts in southern Idaho.

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